Observations on the Protozoa parasitic in Archotermopsis wroughtoni Desn.

Part III. Pseudotrichonympha pristina.

By

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With Plate 10 and 8 Text-figures.

Contents.

INTRODUCTION.

IN previous papers are described species of Protozoa resident in the hind gut of the Indian termite Archotermopsis wroughtoni Desn. It is my purpose here to give an account of a fourth species of these unicellular organisms, already described by Imms (**11**) under the term Tricho-nympha (Holomastigotoides) pristina.

The true name for the animal is undoubtedly Pseudo-trichonympha pristina, but owing to an unfortunate mistake made by Grassi in his earlier papers a good deal of

confusion has arisen around the nomenclature of these forms. In 1910 Hartmann (**9**) gave an account of a flagellate which he named Trichonympha hertwigi, and described male and female forms from which gametes were produced. Conjugation between these gametes was supposed to occur, and the resulting young forms were figured. Hartmann's observations, however, did not bear out these assumptions, and it is certain that they have no foundation in fact. His conclusions were attacked in 1911 by Grassi (**6**), who pointed out that ' Trichonympha hertwigi ' was in reality a mixture of two or more genera, the male form belonging to the genus Holomastigotoides, the female form to the genus Pseudotrichonympha, and the ' young form ' was referred to Pyrsonympha. The ' gametes ' were undoubtedly minute oval flagellates abundant in the intestines of many termites. The confusion arose round the ' male ' and ' female ' forms of Hartmann, for Grassi's description of the genera, to which he referred them, did not appear to agree with Hartmann's account, as Franca pointed out in 1916. In a later paper Grassi (**7**) rectified his error, referring the ' male ' form to the genus Pseudotrichonympha and the ' female ' form to Holomastigotoides, thus reversing his earlier statement. Unfortunately, however, the mistake received a wide acceptance, and even in Doflein's latest edition of his text-book (**3**) it is still perpetrated. Kofoid and Swezy (**18**) also in their recent paper on Trichonympha campanula adhere to Grassi's first classification.

The organism described in the present paper is undoubtedly closely related to the ' male ' form of T. hertwigi, and should therefore be named Pseudotrichonympha pristina and not Trichonympha (Holomastigotoides) pristina, as Imms has called it.

METHODS.

The methods used for the study of P. pristina are those already described in my previous papers (**2**), to which I would refer those interested.

General Considerations.

Systematic Position.

That P. pristina is a flagellate belonging to the order Hypermastigina (Grassi) is indubitable. The Trichonymphidae have suffered much at the hands of systematists. Stein (**26**) in 1878 correctly placed them among the flagellates, though Leidy (**21, 22**) himself considered them as intermediate between the gregarines and ciliates. Kent (**14**) in 1882 founded the family Trichonymphidae and placed it among the holotrichous ciliates, a view supported by Butschli in 1889. Senn (**25**) in 1900 added these forms, as an appendix to the Flagellata ; while Hickson (**10**) allocated them to an appendix of the Ciliata.

In the 1911 edition of Doflein's text-book the classification of Senn was followed ; but in the last edition of 1916 Grassi's correct classification is given.

Finally, in 1913 Poche (**23**) added his quota to the existing confusion by creating the new order Trichonympha, which was placed among the Euflagellata. Kofoid and Swezy (**17, 18**) have recently published papers dealing with the flagellate affinities of these organisms, to which those interested are referred. One point which appears to have escaped notice is the complete absence of a micronucleus in any of the Hypermastigina, a fact which in itself is suggestive of their flagellate affinities, for with a few doubtful exceptions the ciliates are all heterokaryote, as Hickson pointed out in 1903.

P. pristina so differs from Hartmann's male form of T. hertwigi that the two forms cannot be regarded as one species. Grassi distinguishes four species of Pseudotrichonympha, none of which appear to be identical with P. pristina. The descriptions given of the species, however, are so scanty that it is impossible adequately to compare them with the animal described here.

LIVING CONDITION.

Movement and General Appearance.

P. p r i s t i n a is at once striking because of its great swimming power, exceeding that of any other protozoon of this termite.

In living preparations it is a very pleasing sight to observe these animals gliding across the field of view, thrusting away with their anterior flagella the numerous wood particles and other protozoa impeding their progress. This gliding movement, too, is characteristic, resembling that of many of the large ciliates, and doubtless is due to the whole body being supplied with flagella, the anterior of which are probably the main propelling organs, as in T r i c h o n y m p h a c a m - p a n u l a described by Kofoid and Swezy (**18**). During progression the whole of the animal's body revolves on its longitudinal axis, but the direction of revolution is not constant, sometimes occurring clockwise, at others counter-clockwise.

The whole of the body with the exception of the extreme anterior and posterior extremities is covered with flagella, very little differentiated, except that those arising from the peculiar tube-like organ at the anterior end—to be described later—are a little longer than the rest, being 14–16 μ in length, while the remainder are about 12 μ. Also these anterior flagella are much more active during progression. When the animal is stationary, however, the flagella still show movement, the majority independently, but the anterior ones in such harmony that they appear as paired thick bands in whip-like undulation. I was unable to find any indication of a prehensible function in the posterior flagella as described by Kent (**15**) and Porter (**24**). The continuous movement of the flagella, even though the animal is at ' rest ', has been described in T. c a m p a n u l a by Kofoid ; doubtless the function is to keep the body bathed in the intestinal fluid of the termites. In shape the animal is almost oval, but there is a gradual tapering from the anterior to the rounded posterior extremity. There is no sharp demarcation into ectoplasm and endoplasm except at the anterior end, where the proto-

plasm is clearer than that of the rest of the body. The large food particles are aggregated at the posterior two-thirds of the body, and are always found behind the nucleus, as in T r i c h o n y m p h a . This is, however, in sharp contrast to Grassi's experience, for, in his last paper (**7**), he states that in the P s e u d o t r i c h o n y m p h a the food particles are not limited to the posterior extremity, but on occasion may be seen in the region of the anterior organ ' mamella '. Buscalione and Comes (**1**), in their paper, state that when treated with iodine dissolved in iodide of potassium, the region, near to the nucleus, in T r i c h o n y m p h a , gives the characteristic reaction of glycogen, and that this reacting region is sharply defined from the rest of the body. In P. p r i s t i n a , however, the glycogenic reaction is diffused through the whole body, being greatest behind the nucleus. This reaction and the results of other microchemical tests will be fully discussed in a forthcoming paper. As regards the method of food ingestion I can supply no evidence beyond the fact that I have been unable to find any trace of the peculiar process described by Porter (**24**) in T. a g i l i s . Kofoid and Swezy (**18**)— apparently with reluctance—conclude that in T r i c h o - n y m p h a c a m p a n u l a the anterior organ (centroblepharo-plast) may function also as a cytopharynx ; a view also held by Buscalione and Comes. A grave objection to this conclu-sion is that food particles are never found in the anterior region of the body ; Kofoid and Swezy themselves say, ' the anterior region of endoplasm has, in all individuals observed, been entirely free from food bodies or vacuoles, with the exception of small darkly-staining rodlets which may be bacteria or possibly chromidia '. This has been the experience of all workers on T r i c h o n y m p h a , and P s e u d o t r i c h o - n y m p h a p r i s t i n a offers no exception to this rule. As Porter says, ' it seems highly improbable—to say nothing of the absence of any trace of a permanent oral structure—that solid food should pass through this anterior region so quickly that not a single case of its passage, or of its presence in this part, should have been discovered by any of those who have

studied these parasites'. One is thus driven to the belief
that the food is incorporated into the body at the posterior
region, though the method is still unknown.

Morphology.

P. p r i s t i n a is a relatively large animal, its length varying
from 133·9–259·2 μ with a breadth of 60·5–111·2 μ. The
average size may then be taken as 226·3–99·9 μ. In stained
preparations it is evident that the whole of the body flagella
are arranged in longitudinal series (Pl. 10, fig. 1). The extreme
posterior end is, however, naked, and in many preparations
there can be seen a collection of darkly stained bodies, triangu-
larly arranged with the apex directed anteriorly (Pl. 10, fig. 2).
These granules are not to be found in every specimen and
are irregular as regards size, never attaining, however, to that
of the numerous food particles formed in other regions of the
body. From their general appearance and from the fact that
they are always confined to the naked posterior region of the
body, it seems possible that they are of an excretory nature
and that this naked region may be regarded as the physio-
logical anus of the animal. This is, however, a pure conjecture, as
I have found no evidence of granules being ejected from this
region of the body.

Cell Inclusions.

In preparations fixed by Fleming, as modified by Gatenby (**5**)
and then stained by Heidenhain's iron haematoxylin, there
are seen, scattered through the entire plasma, numerous short
deeply-stained rods of a fairly uniform size and thickness
(Pl. 10, fig. 6). In appearance these bodies are very similar to
those found in D i t r i c h o m o n a s t e r m i t e s and described
in a previous paper (**2**). On the other hand they in no way
resemble the cytoplasmic inclusions found in the various
animals investigated by Gatenby (**5**). As I have been unable
to carry out any of the tests requisite for an accurate deter-
mination of the various cell inclusions, I shall content myself
with simply recording their presence in P s e u d o t r i c h o -
n y m p h a p r i s t i n a .

Anterior Organ (Centroblepharoplast).

Pseudotrichonympha pristina terminates at the anterior end in the curious organ found in the Trichonymphidae and described under various names by different observers: thus the Italian workers designate it as 'la bottiglia', 'il cappuccio', or 'il mammillare'; to it Hartmann has applied the term 'Kopforgan', and Porter 'the nipple-like part'. Recently, however, Kofoid and Swezy have identified it as a centroblepharoplast, the name which I prefer to adopt. In P. pristina it is composed of two portions, an inner tube-like one surrounded by a sheath which appears to cover it completely (Pl. 10, figs. 3, 5). This ectoplasmic sheath at its distal extremity becomes continuous with the rest of the body, and this is the only region where differentiated ectoplasm is found. I have been unable to detect any trace of a break in the tip of the sheath such as one would expect were the inner region in reality a tube capable of expelling or taking in liquids as some observers would have us believe. Each anterior flagellum takes origin from a granule situated on the inner surface of the ectoplasmic layer of the centroblepharoplast. These granules are difficult to detect, but in a few suitable preparations they are unmistakably demonstrated (Pl. 10, fig. 5, B.G.). Finally, from the extreme end of the organ there arise two fine threads, which, taking a parallel course down the centre of the endoplasm, diverge at their distal ends to reach the nuclear membrane where they are attached (Pl. 10, figs. 3, 5, S.T.). It seems indubitable that there is such attachment, for in specimens whose nuclei have been thrust out of position the threads are still seen running to the membrane. Thus the nucleus is more or less fixed in position by these threads, in contrast to the 'free' nucleus described by Grassi.

### Striations and Granules.

The striations that are seen crossing the body in a longitudinal series arise from the centroblepharoplast. They consist of ridges in the body surface, and thus broadly agree with those

found in Joenopsis polytricha. Just beneath the
surface of these ridges numerous granules are located, from
each one of which a body flagellum has its origin (Pl. 10, figs. 1,
4, 6, s.r., b.g.). The flagella origins are in the main similar
to those described by Kofoid and Swezy in T. campanula
and Leidyopsis sphaerica, except that I can find no
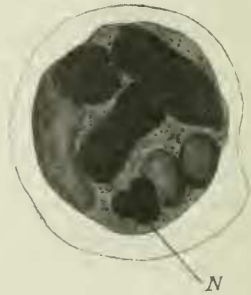trace of oblique fibres running to the granules.

Nucleus.

This body is a large structure situated at the anterior end
of the body and possessing a well-developed membrane, always

TEXT-FIG. 1.	TEXT-FIG. 2.
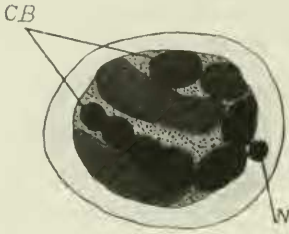
' Resting ' nucleus of P. pristina
showing chromatin blocks em-
bedded in the plastin matrix. Note
the clear peripheral space with the
nucleolus-like body. × 1,880; s.a.,
h.i.h.[1]

Similar to Text-fig. 1, but show-
ing the tripartite nucleolus-
like body. × 1,800; s.a., d.h.

clearly visible (Pl. 10, figs. 1, 3, and Text-fig. 1). Inside the
membrane there is constantly present a clear space, while
the centre of the nucleus is filled with chromatin, in the form
of large irregularly-shaped masses lying in a matrix of what is
probably plastin. The number of chromatin blocks appear
to be quite indefinite (Text-figs. 1 and 2, c.b.). Lying amongst
them there is commonly seen a large body, staining very
deeply with iron haematoxylin, which is sometimes distinctly
tripartite in nature (Text-fig. 2, n.). Unfortunately I have been

[1] For explanation of lettering of text-figures see pp. 263-4.

unable to trace its origin and fate, but that it plays no part
in division is shown by its absence in dividing nuclei. Probably
it is cast out of the nucleus before division takes place. It
appears to have no relation with the curious ' heterochromo-
some ' described by Kofoid in T. c a m p a n u l a .

Division.

As in J o e n o p s i s p o l y t r i c h a the reproductive phases
of P. p r i s t i n a are difficult to find, and I have had to

Text-fig. 3.
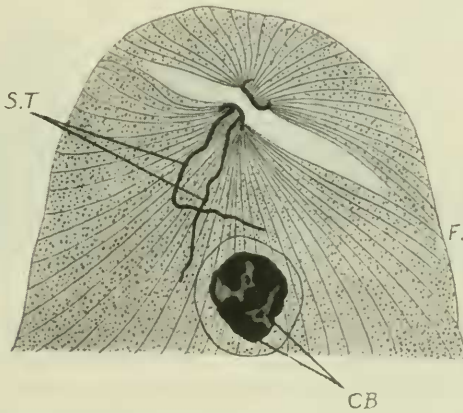
Early stage in the division of P. p r i s t i n a ; the centroblepharo-
plast has separated into two, leaving a split in the protoplasm.
From one of the centroblepharoplasts the threads still persist,
but with their distal ends free from the nuclear membrane.
× 1,000 ; s.a., h.i.h.

examine a large number of preparations to obtain those here
described. Division is initiated by the splitting into two of
the centroblepharoplast. This condition is rarely seen, partly
because it is rare to find an animal so orientated as to render
visible the split blepharoplast. Commonly it becomes inflected
on to the body plasma, thus rendering it very difficult to obtain
a clear picture. In the first stage of the process the two
suspensory filaments become detached from the nuclear

membrane, thus rendering their distal ends free in the plasma ;
subsequently they are absorbed into the body (Text-fig. 3). The
actual divisions of the centroblepharoplast takes place exceed-
ingly rapidly, and I have not seen the intermediate phases.
It seems probable, however, that the splitting originates at
the posterior end and travels forwards, for in a good many
animals the basal region is double, but the anterior one still
single, though obviously much thicker than normal. At
the completion of division the plasma lying between the two
centroblepharoplasts splits, leaving a clear space which is

TEXT-FIG. 4.
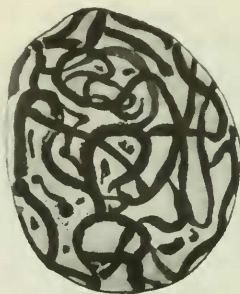
Dividing nucleus with the chromatin in the form of a loose spirene.
× 1,250 ; S.A., H.I.H.

probably the initiation of division of the animal into two
(Text-fig. 3). The whole process recalls that described by Kofoid
and Swezy in T. c a m p a n u l a , and the incomplete descrip-
tion given by Hartmann for his male form of T. h e r t w i g i ;
a paradesmose, however, is not formed between the daughter
centroblepharoplasts in P . p r i s t i n a . As already men-
tioned, the resting—non-dividing—nucleus is composed of large
irregular clumps of chromatin. At the onset of division these
chromatin blocks break up into a number of small rounded
granules embedded in a matrix (Text-fig. 8). Soon the granules
become arranged to form a long spireme, and at this stage the
clear space between the membrane and the chromatin dis-
appears (Text-fig. 4). The nuclear membrane, however, remains

intact, and can be seen throughout the whole process of division. This is contrary to the statement made by Imms. Directly after its formation the spireme is loosely packed together, but subsequently its component parts become more closely aggregated. Finally, it breaks up into a number of long threads, which separate one from the other to form the so-called chromosomes (Text-figs. 5 and 7), and the clear space once more arises. These threads, however, do not appear to split longitudinally, nor can they be seen to be lying together in pairs previous to their separation. During the process just described the nucleus elongates, becoming

TEXT-FIG. 5.
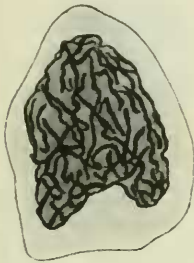
TEXT-FIG. 6.

Nucleus in which the spireme is breaking into individual threads. × 950 ; s.a., h.i.h.

Dividing nucleus with the ' chromosomes ' passing to each pole. Spindle fibres or paradesmose not present. × 1,250 ; s.a. (d.j.), h.i.h.

oval in shape, with the poles somewhat pointed. The long chromosome-like threads now separate into approximately two equal groups, one of which passes to either pole of the elongate nucleus (Text-fig. 6). Further elongation occurs, and at the same time the threads begin to aggregate to form a compact mass, which finally breaks up into irregular chromatin masses to form the daughter nuclei (Pl. 10, fig. 7). Finally, the membrane constricts, dividing in the middle.

This process must take place rapidly, for it is common to find bi-nucleate animals and animals in which the division phase is being initiated, but it is exceedingly rare to encounter the intermediate stages.

As will have been noted, throughout the whole of the division there is no development of spindle fibres, centrioles, or paradesmose.

During the formation of the daughter nuclei the centroblepharoplasts migrate from each other, carrying with them some of the flagella (Pl. 10, fig. 7).
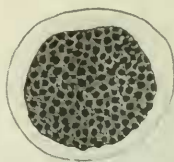
I have been unable to discover the origin of the remaining flagella or that of the suspensory threads to the nucleus.

TEXT-FIG. 7.   TEXT-FIG. 8.

A slightly more advanced stage than the one shown in Text-fig. 5. × 950 ; S.A., H.I.H.

Early stage of nuclear division with chromatin blocks resolved into numerous small granules. × 900; S.A. (D.J.), D.H.

The actual division of the animal into two probably does not occur immediately after the formation of the daughter nuclei, for binucleate animals are commonly encountered in which the plasma shows no obvious sign of splitting.

The division is, however, longitudinal, for the daughter centroblepharoplasts and nuclei always lie in a plane transverse to the axis of the body. This longitudinal division is a further indication of the flagellate relationship of P. pristina.

GENERAL CONSIDERATIONS.

Comparing P. pristina with the other species of Pseudotrichonympha it is evident that, in many respects, it differs markedly from them. The species described by Hart-

mann is larger than P. p r i s t i n a , measuring 760–330 μ by
60–40 μ, and in shape it is more elongated, with well-defined
ectoplasm and endoplasm, the latter divided into internal and
external zones. As in P. p r i s t i n a the body is traversed
with longitudinal ridges from which the flagella takes origin,
but basal granules are not definitely described, though Hart-
mann thinks that they may occur. The chief point of differ-
ence, however, is the centroblepharoplast. In Hartmann's
organism it is composed of three distinct regions : (a) a cylin-
drical tube starting in the ectoplasm and extending to the
endoplasm ; (b) cap, covering the tube ; (c) a second semi-
circular cap covering the whole of the anterior ectoplasm.
Hartmann suggests that the cap represents the true blepharo-
plast, and that the tube is formed of fused basal granules.
Obviously this ' Kopforgan ' is of a more complicated structure
than its homologue in P. p r i s t i n a , and the location of the
basal granules in the ectoplasm and not in ' the tube ' in this
latter organism indicates that Hartmann's suggestion as to the
origin of the ' tube ' is not correct. Grassi's latest description
of the P s e u d o t r i c h o n y m p h a is as follows : ' Body
much elongated and sharpened, with the flagella extending
over the whole of the body, leaving the posterior region naked.
The striations from which the flagella arise are seen running
longitudinally. The nucleus is found in various positions of
the body, and in its ' resting ' stage is composed of a membrane,
peripheral clear zone, and a central mass. The food, consisting
of wood, is not limited to the posterior region of the body, but
is sometimes found in the region of the ' mamella ''.

' The four rods, characteristic of the suspension of the
nucleus in T r i c h o n y m p h a , are not found, and con-
sequently the position of the nucleus is not fixed.'

Grassi distinguishes four species, P. h e r t w i g i var. minor
in C o p t o t e r m e s S j o s t e d d i , P. h e r t w i g i var.
major in C o p t o t e r m e s l a c t e u s , P. m a g n i p a p i l -
l o s a in S c h e d o r h i n o t e r m e s p u t o r i u s , and P. p a r -
r i p a p i l l o s a in S. i n t e r m e d i u s .

The above is sufficient to show that the organism described

the blepharoplast (centroblepharoplast) first divides, followed
by a split in the protoplasm. The chromatin blocks of the
nucleus become resolved into granules, which aggregate to
form a spireme. These phases have been found in P. pristina.
Hartmann's further account, however, of the degeneration
of the primary nucleus and the formation of secondary nuclei,
with the final appearance of gametes, finds no counterpart in
the animal I have investigated. In one important respect
the nuclear division described by Hartmann differs from that
of P. pristina. In this species there is no trace of parades-
mose or spindle fibres, whereas Hartmann figures both these
structures. This is a point of interest, for in all the protozoa
of Archotermopsis, which I have investigated, the
division centres of the nucleus are either absent or poorly
developed.

Thus in Ditrichomonas termites (2) a paradesmose
is formed, but no spindle fibres, centrioles, &c., whereas in other
Trichomonads they are described by Kuczynski (19) and
Kofoid and Swezy (16). In Joenopsis polytricha (2)
nuclear division occurs without any obvious centre, which is
not the case in any of the related animals ; for in Joenia (18)
and Parajoenia (13) a spindle is formed. Finally, as
already noted, the Pseudotrichonymphid described
by Hartmann has a paradesmose and spindle fibres ; as is
also the case in Trichonympha major and minor
described by Foa (4). In P. pristina such structures are
entirely lacking.

Thus in all the protozoa examined from the gut of
Archotermopsis wroughtoni the nuclear division is
very different from that found in related species.

Further, in D. termites the nuclear division and the
locomotor complex is of a more primitive nature than
that described for other Trichonomads ; a statement probably
true for Joenopsis polytricha and Pseudotricho-
nympha pristina. It appears that the protozoa to
which A. wroughtoni is host are in general more primi-
tive than those inhabiting other species of termites. Imms

describes A. w r o u g h t o n i as 'one of the most primitive of living Termites'. The association, therefore, of primitive parasites or 'guests', whichever the case may be, with a primitive host is extremely interesting, and is suggestive that the two groups of organisms have remained associated together for a long period, neither having developed into more complex species, as has occurred with other termites and their associated protozoa.

In conclusion, I wish to express my thanks to Mr. J. B. Robinson for re-drawing for publication, with the exception of figs. 4, 5, 6, and 7, the figures illustrating this paper.

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EXPLANATION OF PLATE 10 AND TEXT-FIGURES.

All the figures are drawn from fixed and stained preparations. The optical apparatus employed was as follows : Zeiss apochromatic oil-immersion objective 2 mm. (N.A. 1·3), and compensating oculars 4, 6, 12, 18. Critical illumination was always employed. The method of fixing and staining, and the approximate magnification is given below in the case of each figure. The following abbreviations are employed : s.A. = Schaudinn's sublimate-alcohol mixture. s.A. (D.J.) = Schaudinn's sublimate alcohol as modified by Dobell and Jepps. Fl. (Gat.) = Fleming's

strong fluid as modified by Gatenby. H.I.H. = Heidenhain's iron-alum haematoxylin. D.H. = Dobell's iron-alum haematein. The lettering of the figures is as follows : B.G. = basal granules. C.B. = chromatin blocks. C.BL. = centroblepharoplast. C.I. = cell inclusions. F.B. = food bodies. N. = nucleolus-like body. S.R. = striations. S.T. = suspensory threads.

Fig. 1.—Stained preparation of Pseudotrichonympha pristina showing ' resting ' nucleus, striations with basal granules, food particles behind the nucleus. × 300 ; S.A. (D.J.), H.I.H.

Fig. 2.—Posterior region of animal with triangular-shaped collection of granules. Note the region without flagella. × 950 ; S.A., H.I.H.

Fig. 3.—Anterior region of P. pristina with centroblepharoplast, from which arise the two threads running to the nuclear membrane. × 950 ; S.A. (D.J.), H.I.H.

Fig. 4.—Portion of a section through body of the animal, showing the ridges (striations) under which are situated the basal granules, the origin of the flagella. × 300 ; Fl. (Gat.), H.I.H.

Fig. 5.—Centroblepharoplast of P. pristina with the threads and basal granules from which the anterior flagella spring. × 1,000 ; S.A. (D.J.), H.I.H.

Fig. 6.—Posterior region of the body, showing the basal granules and flagella. The endoplasm contains unidentified cell inclusions. × 1,000 ; Fl. (Gat.), H.I.H.

Fig. 7.—Top view of a late phase in the division of P. pristina, the centroblepharoplasts are situated at either side of the body with the dividing nucleus between them. Note the absence of any division centre. × 950 ; S.A. (D.J.), D.H.